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CTENOSPONDYLUS NINEVEHENSIS, A NEW SPECIES
 (REPTILIA, PELYCOSAURIA) FROM THE LOWER
 PERMIAN DUNKARD GROUP OF OHIO

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ABSTRACT

A new species of sphenacodontine pelycosaur, *Ctenospondylus ninevehensis*, is described on the basis of disarticulated elements of the skull and postcranial skeleton from the Lower Permian Greene Formation, Dunkard Group of east-central Ohio. This is only the second species of this rare genus to be recognized and the first to be reported from the eastern United States. *C. ninevehensis* existed at the same time or very probably somewhat later than *C. casei*, the other member of this genus, yet its greater primitiveness in a number of features makes it an ideal predecessor to *C. casei*. Geographic isolation by the end of the Pennsylvanian of the Dunkard basin, in which *C. ninevehensis* occurred, from the Midcontinental basin complex, in which *C. casei* occurred, is offered as a possible explanation for the anachronistic appearance of the former. *Ctenospondylus* was most likely already established as a distinct lineage before the beginning of the Permian and, therefore, not a descendant of any of the Early Permian sphenacodontines, such as *Sphenacodon*. It is also improbable that *Ctenospondylus* could have arisen from any of the few poorly known sphenacodontines of the Late Pennsylvanian because of the greater primitiveness of the marginal dentition of *C. ninevehensis*. For these reasons it seems best to take the view that *Ctenospondylus* arose from the haptodontine sphenacodontids at least as early as the Late Pennsylvanian.

INTRODUCTION

Reptiles of the Lower Permian subfamily Sphenacodontinae are considered the most advanced of the order Pelycosauria and closest to the morphological grade of organization of the therapsids, the advanced mammal-like reptiles. *Ctenospondylus* is one of the rarest of the better

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known sphenacodontine pelycosaurs and previously was recognized by only one species, *C. casei*, recorded from only two regions in the United States, north-central Texas and southeastern Utah. It is distinguished from other members of this group mainly by its long, laterally flattened, neural spines that form a high dorsal sail. In addition to *Ctenospondylus*, four other genera comprise the sphenacodontines as follows: *Bathygnathus*, known only from the front part of a skull found on Prince Edward Island, Canada, may be a senior synonym of *Dimetrodon* (Langston, 1963); *Neosaurus*, based on a maxilla from the Jura region of France; *Sphenacodon* and *Dimetrodon*, known from complete skeletons from North America and an upper jaw of the former from England (Paton, 1974). The holotype of *C. casei*, discovered by W. F. Cummins in 1881 in the Lower Permian Belle Plains Formation, Wichita Group of north-central Texas, consists of a complete dorsal vertebra, a dorsal vertebra with partial neural spine, a cervical vertebra lacking the spine, a probable cervical spine, the distal part of a spine, and several fragments of ribs. This specimen was not noted until 1910, however, when Case referred briefly to it and suggested that it be assigned to the European Lower Triassic genus *Ctenosaurus* Huene, a reptile known only from its vertebral column in which the spines are greatly elongated as in *Ctenospondylus*. About a quarter century later the uniqueness of this specimen was recognized by Romer (1936), who named *Ctenospondylus casei*. Further remains of *C. casei* went unreported until Vaughn (1964) discovered many skeletal elements referable to this species in the Lower Permian Organ Rock Shale, Cutler Group of southeastern Utah. Vaughn's descriptions (1964, 1970) included not only portions of the postcranial skeleton, but also, most importantly, the skull. The skull is nearly identical to those of *Sphenacodon* and *Dimetrodon* and provides indisputable evidence that *C. casei* is a sphenacodontine, as well as that it is closely related to these genera.

The specimens described here from the Lower Permian Greene Formation, Dunkard Group of east-central Ohio were first noted by Olson (1975), who referred them to the genus *Ctenospondylus* without specific designation. Examination of the Dunkard *Ctenospondylus* reveals that it represents a new species, herein named *C. ninevehensis*, and that it is more primitive than the contemporaneous, or very likely somewhat earlier, *C. casei*. Despite its late appearance, *C. ninevehensis* is viewed as an ideal, structural antecedent to *C. casei*.

The ancestry of *Ctenospondylus* remains vague. Of the Lower Permian sphenacodontines, only *Sphenacodon*, *Dimetrodon*, and *Ctenospondylus* are known from complete or substantial portions of their skeletons, which are essentially identical except for their distinctly different neural spines. In all three genera the spines are elongated; in *Dimetrodon* the spines are flattened laterally at their bases only, becoming very

long, slender rods distally, whereas the spines of *Ctenospondylus* are intermediate in length between those of *Dimetrodon* and *Sphenacodon* and, as in the latter, have a basically normal, blade-like structure. It might be suggested that the longer-spined *Ctenospondylus* was derived from the shorter-spined *Sphenacodon* as a result of the well-documented evolutionary trend toward disproportional increase in spine length with increase in overall size seen not only in the latter, but in other pelycosaur as well. A *Sphenacodon-Ctenospondylus* lineage cannot be correct, however, because *C. ninevehensis* possesses a more primitive dentition than the oldest and most primitive species of *Sphenacodon*. Features of the maxillary dentition of *Neosaurus* suggest that this poorly known genus was also not ancestral to *Ctenospondylus*. Probably *Ctenospondylus*, as well as *Sphenacodon*, represented independent lineages during the Early Permian. The few incompletely known sphenacodontines of the Late Pennsylvanian are also eliminated as possible ancestors of *Ctenospondylus* because of their more advanced dentitions than that of *C. ninevehensis*. It is suggested that *Ctenospondylus* became established as a separate evolutionary line by the Late Pennsylvanian or earlier, most likely stemming from the Late Pennsylvanian-Early Permian haptodontine pelycosaur, which are generally considered as ideal predecessors of the sphenacodontines and as probably having an antiquity that extends back to the Early or Middle Pennsylvanian.

The greater primitiveness of *C. ninevehensis* over the contemporaneous or probably earlier-occurring *C. casei* is explained as the result of isolation. Paleogeographic reconstructions suggest that the Dunkard basin, once the terminal portion of a northeastern arm of the Midcontinental seaway, became widely separated from the Midcontinental basin complex at the end of the Pennsylvanian by the continued growth of a vast, intervening area of low relief occupying the continental interior.

The following abbreviations are used to refer to repositories of specimens: AMNH, American Museum of Natural History, New York; NTM VP, Navajo Tribal Museum, Window Rock, Arizona; MCZ, Museum of Comparative Zoology, Harvard University.

SYSTEMATIC PALEONTOLOGY

Class Reptilia

Order Pelycosauria

Family Sphenacodontidae

Subfamily Sphenacodontinae

Genus *Ctenospondylus* Romer, 1936

Ctenospondylus ninevehensis, new species

Holotype.—MCZ 3386 consists of the following disarticulated elements of the skull, lower jaw and postcranial skeleton: premaxillae, left

maxilla and small part of right, right prefrontal, probable right jugal, left pterygoid, left dentary, axial neural spine, three dorsal vertebrae and spine, lumbar vertebra, four caudal vertebrae and probable spine, three cervical ribs and parts of cervical and dorsal ribs, part of scapular blade, left humerus and distal end of right, and right pelvis. The holotype, as well as the referred specimen, were collected by Dr. Donald Baird of Princeton in June 1955.

Referred specimen.—MCZ 4458, a right maxilla.

Horizon.—Lower Permian Nineveh Limestone, Greene Formation, Dunkard Group.

Locality.—Clark Hill on County Route 43, 1.1 miles west of junction with State Route 7, sec. 16, Salem Township, Monroe County, Ohio.

Diagnosis.—All the features that distinguish *Ctenospondylus ninevehensis* from *C. casei* express a more primitive grade of organization in the former; these include: 1) a greater number of marginal teeth, consisting of four premaxillary, 21 maxillary, including three precanines, and an estimated 31 dentary teeth; 2) relative length of neural spine of dorsal vertebra about 23% shorter; 3) axial neural spine of the more generalized sphenacodontine shape; 4) smaller overall body size.

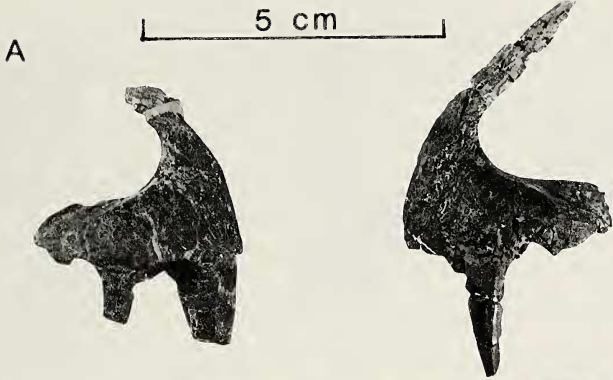
Etymology.—Name refers to the stratigraphic unit in which the specimens were found.

Description

Cranial elements.—Cranial elements of the holotype include right and left premaxillae, left maxilla and small part of right, right prefrontal, probable right jugal, left pterygoid, and left dentary. The reasons for believing that these elements, as well as those described below as belonging to the holotype, came from one individual is their discovery close together, their appropriateness in size to one another, and the absence of duplicate elements of the same size or evidence of the presence of any additional pelycosaur species. A right maxilla, MCZ 4458, is also referred to *C. ninevehensis*. Both the right and left premaxillae (Fig. 1) are nearly complete and possess spaces for four teeth, which is one or two more than is seen in most of the sphenacodontine pelycosaurs. The teeth appear to have been alternately replaced, so that only two functional teeth are present in each premaxilla; further, the tooth replacement sequence of one premaxilla alternates with that of the opposite side. In the right premaxilla only the basal halves of the first and third teeth are preserved and the second and fourth are represented by empty sockets, whereas in the left the second tooth is nearly intact, the fourth has been broken off at the base and the first and third sockets are empty except for the tip of a replacement tooth seen in the third. Judging from what is preserved of the functional teeth and the sizes of the unoccupied sockets, the size relationships of the premaxillary teeth are of the typical sphenacodontine pattern; the teeth decrease in size considerably posteriorly, with the anterior pair being much larger than the posterior pair. The teeth

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Fig. 1.—*Ctenospondylus ninevehensis*, new species A, right and left premaxillae, B, left maxilla, and D, left dentary of holotype MCZ 3386. C, right maxilla of referred specimen MCZ 4458.



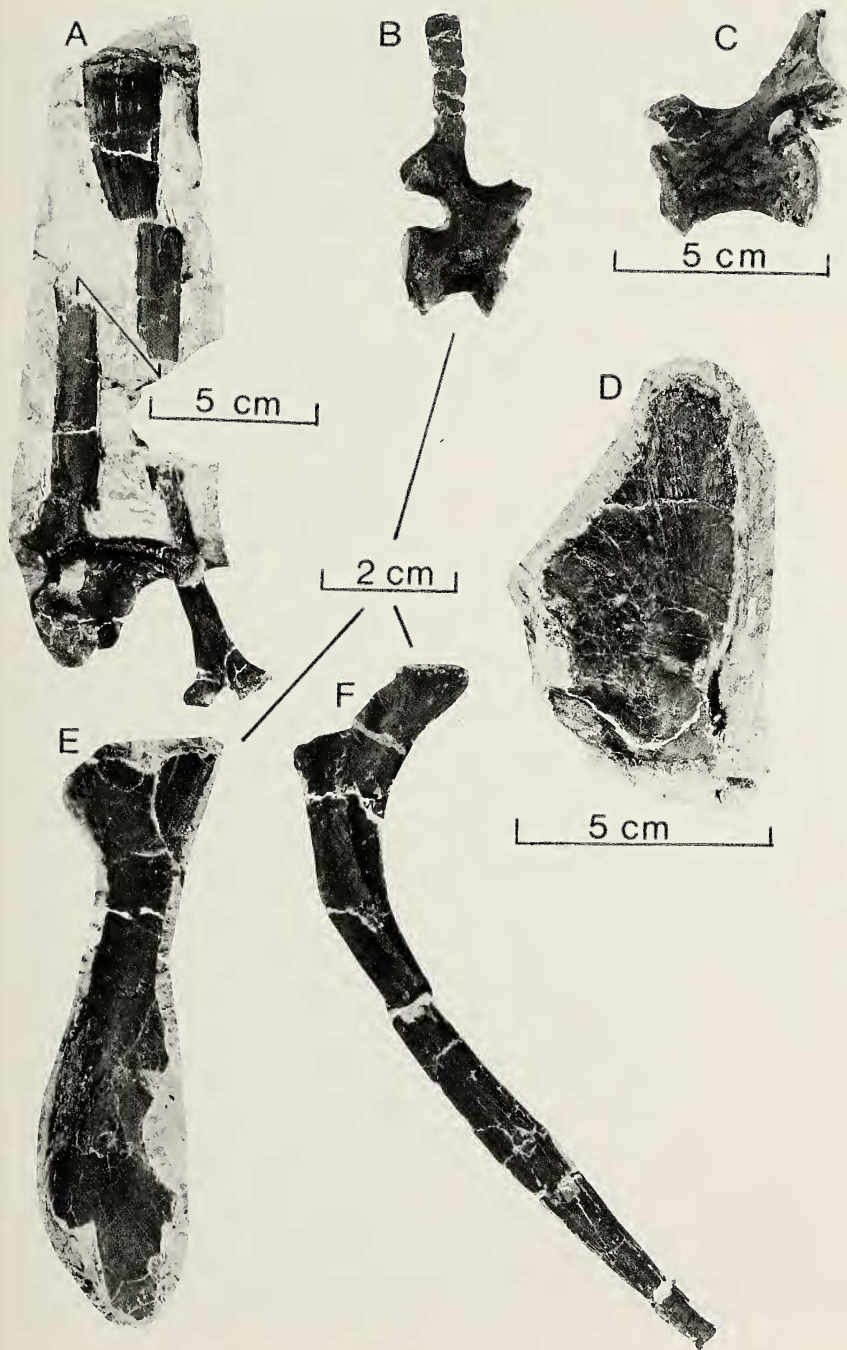
are subcircular in cross-section and exhibit only a slight development of anterior and posterior cutting edges. The holotypic left maxilla (Fig. 1) is complete along its lightly convex, ventral margin and has a maximum length of 133 mm; the upper half of its dorsal lamina is missing. Sixteen teeth are preserved and there are spaces for five more, giving a total of three precanines, two canines, and 16 postcanines. The precanines decrease in size anteriorly from a maximum length of 14 mm; the canine pair are nearly equal in size and measure 25 mm in length; the first postcanine is slightly smaller than the posteriormost precanine and the second postcanine (missing) is presumed to have been smaller as in the referred right maxilla MCZ 4458 (Fig. 1); the remaining postcanines exhibit a steady decrease in size posteriorly from a maximum length of about 13 to less than 4 mm. In sphenacodontid fashion all the teeth are slightly to moderately recurved and laterally compressed with moderately developed, nonserrated, posterior cutting edges; postcanines 8 through 21 are slightly bulbous compared to the other teeth. There is a moderate swelling of the maxilla above the canine pair and anterior to the precanines the ventral margin of the maxilla is only very slightly arched dorsally, forming a very weakly-developed maxillary "step." The referred right maxilla MCZ 4458 (Fig. 1) is essentially complete and except for a couple of very minor differences that are undoubtedly related to its smaller size (length 106 mm) is identical to that of the type. The two canines appear to be relatively slightly smaller, with the anterior one, though not complete, being definitely larger; its maxillary step and lateral canine swelling are also less pronounced than in MCZ 3386.

The holotypic right maxilla is represented by only a small, poorly preserved portion of its anteroventral margin that contains a canine pair and a precanine that match exactly in size and character those of the left maxilla. The greater portions of the right prefrontal and what appears to be a right jugal exposed in medial view are preserved and are not unlike those of other sphenacodontines. All that remains of the left pterygoid is the proximal portion of the palatal ramus and almost all of the thickened, ventral ridge of the quadrate ramus. The transverse flange is well developed with five of the 10 or more teeth it possessed preserved; the largest of these teeth, located at the center of the series, is about 8 mm in length. The palatal ramus is covered by very small denticles; however, about 15 mm anterior to the transverse flange and close to the medial border of the palatal ramus begins a narrow cluster of relatively much larger denticles, reaching a maximum diameter of about 1.7 mm, that extends about 10 mm to the anterior broken margin of the pterygoid. In all these features the pterygoid of the holotype closely approximates that seen in the reconstruction of the skull of *Dimetrodon limbatus* by Romer and Price (1940:501, Pl. 13).

The left dentary (Fig. 1) as preserved measures 125 mm in length and is missing approximately its posterior fourth, which undoubtedly included a small part of the marginal dentition. The tooth-bearing margin of the dentary is slightly concave except at its very anterior end, where it slants somewhat downward. There are 19 preserved teeth of which only the posteriormost two are incomplete and there are gaps for six more. The total number of marginal dentary teeth was, however, almost certainly greater than 25, judging from the dental counts given by Romer and Price (1940:434, Table 2) for specimens of various species of *Sphenacodon* and *Dimetrodon*. The dental counts in-

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Fig. 2.—*Ctenospondylus ninevehensis*, holotype, MCZ 3386. A, posterolateral view of anterior dorsal vertebra (displacement of spine indicated) and posterior view of proximal half of spine of a preceding dorsal; B, right lateral view of mid-caudal vertebra; C, left lateral view of distal caudal; D, left lateral view of axial neural spine; E, anterior view of atlantal or possibly axial rib; F, posterior view of left cervical rib.



dicate that in sphenacodontines the dentary typically possesses about 50% more teeth than the maxilla. On the basis of this formula, the presence of 21 teeth in the maxilla of the Dunkard *Ctenospondylus* suggests that the actual number of dentary teeth may have been about 31. All the teeth are slightly to moderately recurved and laterally compressed with fairly sharp, nonserrated, posterior edges. In sphenacodontine fashion there are a few teeth very near the anterior end of the jaw that are much enlarged over the rest of the series. In this case three enlarged teeth of essentially identical development and measuring 13 mm in length occupy positions 3, 4, and 5. Missing tooth 2, judging from its empty socket, must have been somewhat larger than tooth 1, which measures 8 mm in length; that part of the series containing teeth 6 to 14 shows great variation in size, with teeth ranging in length from 5 to 8 mm; teeth 15 to 25 diminish slightly in size posteriorly from a maximum length of 7 mm and exhibit a slightly stouter outline than the other teeth of this size range.

Vertebrae and ribs.—Elements of the vertebral column identified as belonging to MCZ 3386 include an axial neural spine, three dorsal vertebrae and a dorsal neural spine, a lumbar vertebra, four caudal vertebrae and a probable caudal neural spine, and three cervical ribs and parts of cervical and dorsal ribs. The axial neural spine (Fig. 2) is essentially complete, exposed in left lateral view and includes a small, proximal portion of the anterior and most of the posterior zygapophyses of this side. In outline the spine conforms very closely to those of *Sphenacodon* and is also not greatly unlike those of various species of *Dimetrodon* (Case and Williston, 1913; Romer and Price, 1940; Vaughn, 1964). In comparison with these genera the holotypic spine differs mainly in not becoming greatly thickened toward its posterior margin. The height of the spine is about 74 mm measured above the posterior zygapophysis along a line parallel to its posterior edge. In sphenacodontid fashion the anteroventral margin projects over the anterior zygapophysis, from which it is separated by a narrow, deep notch.

The three vertebrae and neural spine from the dorsal region of the column include a complete vertebra and the proximal half of a spine found closely associated with it (most likely belonging to the preceding vertebra) that are probably from the anterior part of the series (Fig. 2) and two vertebrae, consisting mainly of the centrum and the base of the neural spine, believed to be from the middle and posterior parts of the series. All are of sphenacodontid style. The lateral surface of the neural spine just above the transverse process is deeply excavated. The zygapophyses are steeply tilted downward and inward and do not extend laterally beyond the margin of the centrum. The lateral surface of the centrum is deeply concave, flaring outward at the ends of the centrum to form an expanded, subcircular rim surrounding the notochordal funnel. The ventral longitudinal keel of the centrum is sharply pinched and in lateral view is slightly concave, reaching the ventral margins of the centrum rims, which are expanded downward as relatively flat lips for articulation with the intercentra. The dorsals, as well as the lumbar and caudal vertebrae described below, exhibit well developed anterior centrosphenes and posterior centrantra on the dorsal margins of the centrum rims. In all of the vertebrae there is also a ventral beveling of the ends of the centra to accommodate the intercentra; this feature, which is much more pronounced at the anterior end of the centrum, becomes less prominent toward the posterior end of the column. Standard measurements for the vertebrae of the holotype are given in Table 1.

The preservation of the complete anterior dorsal vertebra (Fig. 2) is fortunate inasmuch as it is the character of the neural spine that provides the basis for identifying the holotype as belonging to the genus *Ctenospondylus*. Although two parts of the neural spine have been displaced small distances along fracture planes, the height of the spine above the posterior zygapophyses can still be accurately measured as 152.4 mm. The spine is laterally compressed, with an anteroposterior length of about 14 mm from just above the buttresses of the posterior zygapophyses to about a third the height of the spine, then constricts to about 12 mm for a very short distance before slowly expanding

Table 1.—Measurements (in mm) of various vertebrae of *C. ninevehensis*, holotype, MCZ 3386; dorsal vertebrae of *Ctenospondylus* aff. *C. casei*, NTM VP 1014 from southeastern Utah (Vaughn, 1964); and *C. casei*, holotype, AMNH 4047 from north-central Texas (Romer and Price, 1940). 1, greatest length of centrum; 2, width of centrum at posterior end (anterior end for NTM VP 1014); 3, height of centrum at posterior end; 4, orthometric linear unit value (radius of centrum to the $\frac{2}{3}$ power; see Romer and Price, 1940); 5, spine length; 6, spine length in orthometric linear units.

Specimen and vertebrae	1	2	3	4	5	6
MCZ 3386						
anterior dorsal	24.5	21.3	24.3	4.8	152.4	31.7
mid-dorsal	27.2	20.0	20.0	4.6		
posterior dorsal	27.0	13.7	22.2			
lumbar	19.5	15.5	14.7			
proximal caudal	18.0	15.9	16.0			
proximal caudal	17.6	15.5	14.2			
mid-caudal	18.0	14.8	13.8			
distal caudal	17.0	10.0	9.5			
NTM VP 1014		22.0		4.9	211.0	42.5
AMNH 4047	34.0	31.0	33.0	6.2	245.0	40.0

to 23 mm at its distal end. In transverse width the spine is about 10 mm just above the buttresses of the posterior zygapophyses and 8 mm at its summit. The basal third of the spine bears fore and aft grooves and ridges, which appear to be more pronounced on the anterior face; at about the level where the spine is narrowest anteroposteriorly these grooves are replaced by rounded margins. The transverse process is well developed and extends 40 mm laterally out from the midline, is directed slightly downward and backward, is roughly triangular in cross section with the apex directed downward, is broadly concave ventrally in end view, and exhibits a rather deep excavation on the posteroventral surface of its base. The articular facet is egg-shaped in outline with the narrower end pointing ventrally and faces ventrolaterally and slightly posteriorly. The line of juncture between the arch and centrum is detectable only as a roughened ridge. By way of comparison with the vertebra described as an anterior dorsal, the vertebra believed to be a mid-dorsal is judged so by differences in its transverse process. The process is shorter, measuring 32.7 mm out from the midline, and extends directly laterally. Its articular facet is triangular in outline with the apex pointing downward and faces ventrolaterally; the apex of the facet is formed by the end of a thin ridge that extends along the ventral length of the process. The presumed posterior dorsal vertebra has undergone lateral crushing, which is most obviously reflected in its relatively very narrow centrum width. The transverse process is short, about 5 mm, and in cross section is narrowly oval with anteroposterior elongation. Its articular facet is also oval and faces laterally and very slightly ventrally. A slightly raised, subcircular facet for the capitulum of the rib is seen high up on the anterior rim of the centrum.

The single, presumed lumbar vertebra consists essentially of the centrum and the base of the neural spine. The base of the spine is about 8 mm in anteroposterior length and is only very slightly excavated laterally. The transverse process, or diapophysis, is positioned on the upper half of the centrum, is oval in cross section with its long axis directed anterodorsally, and projects outward from the centrum just barely at its anterior edge to about 5 mm at its posterior edge. Its oval articular surface extends from a point near the upper margin of the anterior rim of the centrum posteroventrally to a little

beyond the mid-length of the centrum and faces laterally and slightly anteriorly. The parapophysis is considerably smaller than the diapophysis, appears as a slightly raised, vertically elongated oval area located beside the anterior rim of the centrum and is separated from the diapophysis by a very narrow channel for the passage of the segmental artery; its articular surface faces ventrolaterally. The lower half of the lateral surface of the centrum is lightly excavated and the ventral, longitudinal keel is weakly developed.

The four caudal vertebrae of the holotype include two from the proximal and one each from the middle and distal regions of the tail. The proximal caudals consist for the most part of the centrum and the base of the spine. The spines are laterally compressed and only slightly excavated at their bases. In anteroposterior length the spine of the larger vertebra is 9 mm, whereas that of the smaller one is about 7.3 mm. Enough of the spines are preserved to indicate that they were inclined slightly anteriorly. In both proximal caudals the transverse processes are for the most part preserved and probably include very small portions of the fused ribs. The process has a broad base, extending across the upper half of the centrum from the anterior rim to within a short distance of the posterior rim, and projects ventrolaterally. A well-developed ridge extends upward from the lateral edge of the anterior rim of the centrum to buttress the process along the anterior margin of its ventral surface. The mid-caudal vertebra (Fig. 2) lacks essentially only the posterior zygapophyses and portions of the anterior zygapophyses. The neural spine is about 24 mm high, measured above the posterior zygapophyses, is moderately excavated at its base, and curves very slightly posteriorly. In anteroposterior length the spine is 5.2 mm just above the buttresses of the posterior zygapophyses, then gradually expands to 5.7 mm at its termination. The transverse process is reduced to a low protuberance high up on the centrum and somewhat anterior to its mid-length; posterior to the process is a rather deep, dimple-like depression. The incompletely preserved ventral keel of the centrum is represented by a low ridge. The distal caudal vertebra (Fig. 2) is complete except for the tip of the spine and very small portions of the anterior zygapophyses. The spine is inclined slightly posteriorly and tapers to what was probably a blunt point. Excavation of the neural arch at its base is reduced to a slight depression and the median ventral keel or ridge has been replaced by a narrow, flat surface. An isolated, laterally flattened neural spine that is complete to just below the posterior zygapophyses but incomplete distally has been catalogued with the holotype as probably belonging to a proximal caudal. As preserved it extends 23.4 mm above the posterior zygapophyses, has an anteroposterior length of 7.8 mm just above the buttresses of the zygapophyses, but expands distally to about 10.2 mm.

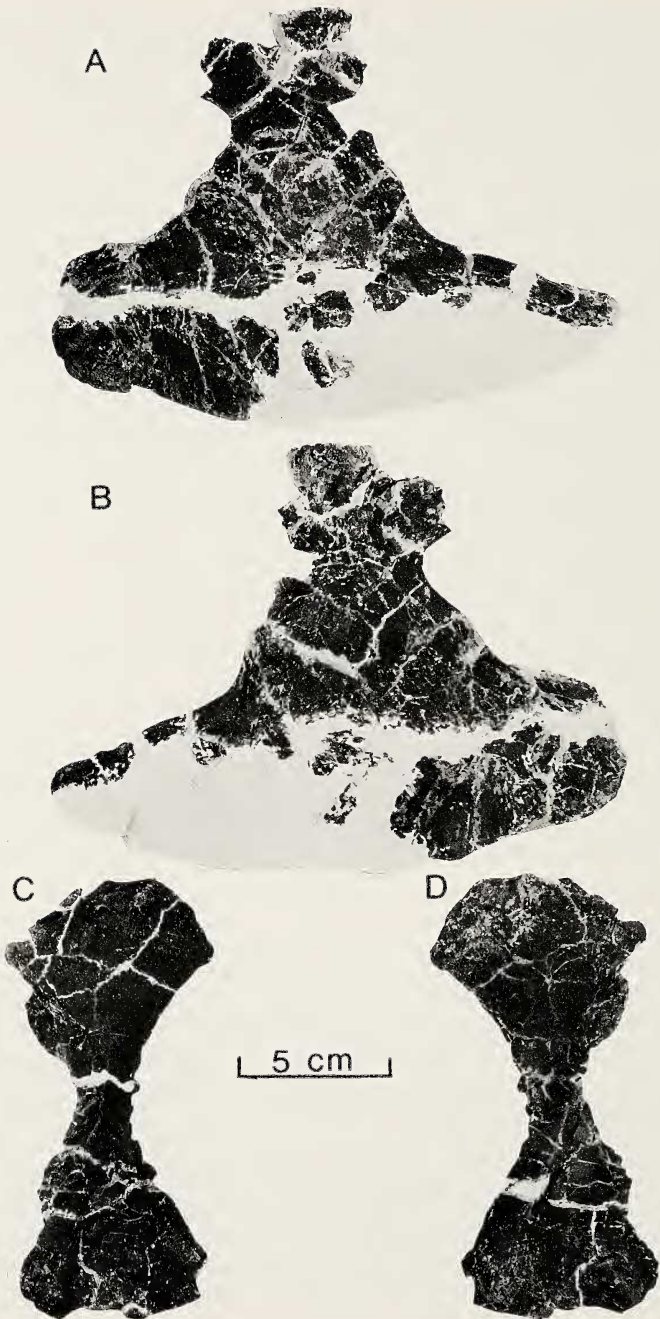
One of the three complete or nearly complete cervical ribs (Fig. 2) of MCZ 3386 is suspected of belonging to the atlas or possibly the axis. In this rib the capitulum and tuberculum appear to be about equally developed, are set close together, and meet at an angle between them of about 35°. There is a small gap in the triangular sheet of bone connecting the two heads that is probably due to imperfect preservation and the rib can, therefore, be described as holocephalous. Unusual is the very thin, paddle-like expansion of the distal portion of the rib shaft. Romer and Price (1940) point out that in ophiacodonts there is some development of a flat, paddle-like blade of the cervical rib shaft for attachment of the levator and anterior serratus muscles supporting the scapula; they also see some evidence of a similar condition in edaphosaurs. Further, their figures (Romer and Price, 1940:299, Fig. 58) of the primitive sphenacodontid *Haptodus* show a distal dialation of the anterior cervical ribs. However, they state that among the more advanced sphenacodontids there is no distal expansion of the cervical ribs. They note that the first seven cervicals of *Dimetrodon* end in pointed tips, but do not comment on *Sphenacodon*, for which this information is apparently lacking. It is interesting that Vaughn (1964) has described a fragmentary cervical rib in *Ctenospondylus* that is somewhat expanded distally. As preserved the presumed axial or atlantal cervical rib of *C.*

ninevehensis is 81 mm long, 19.8 mm wide at its proximal end, 8.8 mm wide at its narrowest point just distal to the union of the rib heads, and about 19 mm across the widest point of its distally expanded shaft. Because the distal portion of the rib is incompletely preserved, the actual maximum width and length of the rib are at least slightly greater than the measurements given above. Although the proximal ends of the other two cervical ribs (Fig. 2) are somewhat incomplete, they also appear to be at least nearly holocephalous. Their shafts are essentially complete and are typically sphenacodontid in being slender and oval in cross-section, and in having pointed ends. The smaller and presumably more anterior of the two ribs is 105 mm long, 27.8 mm wide at its proximal end, and about 8 mm wide at about mid-length of the shaft; the same measurements for the larger rib are 131, 26, and 8 mm respectively. Among the materials assigned to MCZ 3386 are portions of rib shafts and a poorly preserved proximal end of a dichoccephalous rib that was undoubtedly from the dorsal region of the column.

Appendicular elements.—All that remains of the appendicular skeleton of the holotype is a small part of a scapular blade, a nearly complete left humerus, the distal end of a right humerus, and the greater part of a right pelvis. These elements exhibit no marked differences from those of the advanced sphenacodontids *Dimetrodon* and *Sphenacodon* and they need not be described in detail here (see Romer and Price, 1940, for descriptions and illustrations). The left humerus (Fig. 3) lacks mainly the supinator process and the posterodistal margin of the entepicondyle. It has undergone some dorsoventral crushing, but still retains a slight twisting of the proximal and distal planes. The rugosities and muscle scars are well developed, suggesting a fully adult individual. As preserved, the humerus is 142.7 mm long, 69 mm wide across the proximal end, 62.1 mm across the distal end, and has a minimum dorsoventral thickness through the narrowest portion of the shaft of 11.3 mm. Important areas missing in the right pelvis (Fig. 3) include the posterior extension of the dorsal blade of the ilium, a very small amount of bone along the posterior end of the ischium, and that part of the pubis contributing to the puboischial plate. As preserved the ilium is 82.5 mm high, 42.4 mm across the neck, and 58.5 mm across the base, the pubis is 101 mm long, and the ischium is 80 mm in length and height. In overall proportions the only noteworthy difference I can detect between the pelvis of MCZ 3386 and those of most sphenacodontids is the relatively shorter length of its ischium compared to that of the pubis. This is true, even if one takes into account that a very small amount of bone is missing along the posterior margin of the ischium. In advanced sphenacodontids the length of the ischium normally exceeds that of the pubis by about 10%; the reverse appears to be the case in MCZ 3386.

COMPARISONS

Generic assignment of MCZ 3386 to *Ctenospondylus* is based solely on the shape and length of the neural spine of its dorsal vertebrae. In the absence of this structure it would be almost impossible to determine whether MCZ 3386 pertains to *Ctenospondylus*, *Sphenacodon*, or *Dimetrodon*, because their skeletons are otherwise essentially identical. Though Vaughn (1964, 1970) has recently found some additional differences in detail of the dermal skull roof, braincase, and the atlas-axis complex of these three genera, the neural spines remain as the major feature for distinguishing them. In *Dimetrodon* the spines are of the normal, laterally flattened shape for only a short distance above the neural arch, then abruptly change to slender, transversely expanded rods having fore and aft grooves that give them a figure-8 shape in



cross-section. These spines supported a very high sail-like structure, which in terms of the orthometric linear units of Romer and Price (1940:8)—one linear unit is defined as equal to the radius of the centrum to the $\frac{2}{3}$ power—reached a maximum length in various *Dimetrodon* species of from 90 to 156 units. In *Sphenacodon* and *Ctenospondylus* the neural spines are flat from side to side for their entire length and are also elongated, but far less so than in *Dimetrodon*. It is the degree of spine elongation that distinguishes *Sphenacodon* from *Ctenospondylus*; in the only two described North American species of the former, dorsal spine length ranges from about 14 to about 20 units, whereas in *C. casei* it has been calculated at approximately 40 units (Romer and Price, 1940) and slightly greater (Vaughn, 1964). Spine length in the only complete dorsal of *C. ninevehensis*, believed to be an anterior dorsal, is about 32 units (Table 1) and is, therefore, intermediate in length between those of *Sphenacodon* and *C. casei*.

In using spine length as a diagnostic feature in pelycosaurs it is necessary to take into account two important and closely related evolutionary trends seen in many of the better known genera—1) progressive increase in body size, and 2) disproportionate increase in spine length with increase in overall body size. Considering these trends, the greater spine length of *C. ninevehensis* over that of *Sphenacodon* is even more impressive if the comparison is limited to a species of the latter of comparable overall size. The only *Sphenacodon* species that are based on essentially complete skeletons are *S. ferox* and *S. ferocior* of North America (the Lower Permian species *Oxyodon britannicus* Huene, based on a maxilla from England, has been reassigned to *Sphenacodon* by Paton [1974] and represents the only other recognized member of this genus); both species are known from the Lower Permian of the Four Corners region of southwestern United States, and the considerably smaller *S. ferox* occurs at a somewhat lower horizon than *S. ferocior* (Romer, 1960; Vaughn, 1964). Most important, however, in *Sphenacodon*, as well as in *Dimetrodon*, there is a disproportionate increase in spine length with the increase of other linear measurements (Romer, 1948) and as noted by Romer and Price (1940), though *S. ferocior* is about 20% larger than *S. ferox* in size, it exhibits an increase in spine length of about 45%. The sizes of the centra and cranial elements, particularly the maxilla, of *C. ninevehensis* indicates an overall size well within the size range of *S. ferox*,

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Fig. 3.—*Ctenospondylus ninevehensis*, holotype, MCZ 3386. A, lateral, and B, medial views of right pelvis. C, dorsal, and D, ventral views of left humerus.

yet the dorsal spine length in the former is over 30 units, as compared to only about 14 units in the latter.

Judging from the data in Table 1, disproportionate increase in neural spine length with increase in overall size is not obvious in *Ctenospondylus*. Specimens of *C. casei* have been collected from the Lower Permian in two widely separated areas; the holotype AMNH 4047, based on a few vertebrae and rib fragments, is from north-central Texas (Romer, 1936), whereas several specimens referable to this species, including a skull and the characteristic vertebrae, have been described (Vaughn, 1964) from southeastern Utah. As noted by Vaughn (1964), though the dimensions of the one nearly complete, isolated dorsal vertebra from the Utah materials, NTM VP 1014, are considerably smaller than those of the complete dorsal of the Texas specimen, in terms of orthometric linear units (Table 1) their neural spines are very close in relative length. Because the Utah and Texas specimens are indistinguishable morphologically, so few in number, and are from deposits of equivalent age, Vaughn (1964) felt it best to refer the Utah specimens to *C. casei*, though he was aware that their difference in size and wide separation geographically raises the possibility that they may represent different species. In light of the tendency for disproportionate spine growth with increase in overall size in many pelycosaur, the nearly equal relative lengths of the spines in the Utah and Texas forms could be viewed as indicating that their difference in overall size merely reflects a difference in growth stages of a single species. Whether or not the Utah *C. casei* represents a subadult stage of growth, it is significant that, although its overall size was probably only a little greater than that of *C. ninevehensis*, its neural spines are about 8 units longer. This comparison, however, is based on what is believed to be an anterior dorsal vertebra of *C. ninevehensis*, and had it been possible to use a vertebra of more average dimensions for the presacral column, such as a mid-dorsal, this difference may not have been as great. For instance, a relatively longer neural spine is suggested by the one mid-dorsal centrum identified in the holotype of *C. ninevehensis*. In contrast to the anterior dorsal centrum used to calculate relative spine length in the Dunkard species, the width of this centrum is less, giving a slightly smaller orthometric linear unit value, and its missing spine was probably at least a little longer, assuming that the spines reached a maximum length toward the middle of the presacral column. It is possible that the spines in *C. ninevehensis* may have reached about 35 units in length.

On the basis of relatively shorter neural spines and possibly smaller overall size the Dunkard *Ctenospondylus* can be considered not only a distinct species, but more primitive than *C. casei*. This conclusion is reinforced by differences in other features, particularly their denti-

tions. Because the sphenacodontines exhibit a general trend toward reduction of the marginal dentitions of the upper and lower jaws, the exceptionally large number of teeth in *C. ninevehensis* as compared with *C. casei* (Vaughn, 1970), which has a typical complement of marginal teeth, can be taken to mean that the former is not only more primitive than the latter, but also occupies a very primitive position within the Sphenacodontinae. The four premaxillary, 21 maxillary and the estimated 31 dentary teeth in *C. ninevehensis* represent counts equal to, or just under, the largest of those recorded for any of the sphenacodontines (see Romer and Price, 1940:Table 2). In contrast, the reconstructed skull roof of *C. casei* by Vaughn (1970) shows three premaxillary and 14 maxillary teeth with gaps for possibly two more; information on the lower jaw dentition was not given. Among the sphenacodontines presence of three premaxillary incisors is the general rule, but in some the number has been reduced to two, and only in the very small and primitive *Dimetrodon natalis* are there four. Similarly, the presence of three well-developed precanines in *C. ninevehensis* can be considered primitive; in the sphenacodontines three precanines are rare, two or one being typical, and in some they are absent. In Vaughn's (1970) reconstruction of the skull of *C. casei* two precanines are restored, but the gap seen immediately in front of the canines could have held a third precanine. Of the two North American species of *Sphenacodon*, the smaller, somewhat more primitive, *S. ferox* has a greater number of marginal teeth with maximum tooth counts of three premaxillary, 16+ maxillary, two of which are precanines, and 24 dentary teeth; *S. ferocior* shows a more advanced condition in having three premaxillary, 14 maxillary with loss of all the precanines, and approximately 21 dentary teeth. It can also be noted that, as in the skull of *C. casei*, the "step" at the anterior end of the maxilla in *C. ninevehensis* is not as pronounced as it is in *Sphenacodon* or the majority of the species of *Dimetrodon* (see Romer and Price, 1940:Figs. 4, 5).

The axial neural spine of *C. casei* is known only in the Utah materials described by Vaughn (1964) and is not only quite different from *C. ninevehensis*, but somewhat unique as revealed by his comments (1964:580) that "The posterior surface of the axial neural spine seems to have been deeply concave, but preservation is not good in this region. The posterior border of the spine meets the dorsal border at a large, semicircular notch, unlike any other sphenacodontid axis I have seen figured." Inasmuch as the axial neural spine of *C. ninevehensis* is very much like those of *Sphenacodon* and many of the species of *Dimetrodon*, such as *D. milleri* and *D. limbatus* (see Romer and Price, 1940), it seems safe to say that in this feature *C. ninevehensis* is also more primitive than *C. casei*.

DISCUSSION

Ctenospondylus ninevehensis presents the unusual situation of being considerably more primitive than *C. casei*, but occurring at an equivalent or very probably somewhat higher stratigraphic level. Vaughn (1964) correlated the vertebrate-bearing beds of the Organ Rock Shale, Cutler Group of Utah and Arizona, from which came the specimens he referred to *C. casei*, with the upper part of the Wichita Group of the Lower Permian terrestrial section of north-central Texas; the type of *C. casei* is from this part of the Texas section, the Belle Plains Formation. Following the correlations of Dunbar et al. (1960) and McKee, Oriol et al. (1967), which differ only slightly, the age of the Texas and Utah specimens of *C. casei* can be considered as earliest Leonardian. Though controversy surrounds the biostratigraphic placement of the Dunkard Group, opinions based on plants, invertebrates, and vertebrates are that it is on the whole Lower Permian (Barlow, 1975). Olson (1975) views the Dunkard vertebrate assemblage as most likely being equivalent to the Admiral and Belle Plains Formations of the Wichita Group and, thus, close to the Wolfcamp-Leonard boundary. Attempts at correlating specific horizons within the Dunkard, however, have drawn less attention. A consideration of the vertebrates from the Washington Formation, the lower of the two Dunkard formations, led Berman and Berman (1975) to conclude that they allow a range of possible correlations with the Lower Permian of Texas from about mid-Wichita up through the overlying Clear Fork Group. This in turn suggested an equivalence with either the upper part of the Wolfcampian or the base of the Leonardian Series. Using this correlation as a guide, the Nineveh Limestone, which occupies a level approximately a little more than a third of the way up through the overlying Greene Formation, can almost certainly be judged as being basal Leonard or higher. Lund (1975) has attempted to recognize vertebrate biostratigraphic zones from about mid-Allegheny Group up through the Conemaugh and Monongahela Groups to the top of the Greene Formation of the Dunkard. He presents evidence to suggest that the Greene Formation may be equivalent to the basal Leonardian lower Clear Fork beds of Texas.

Despite its late appearance, *Ctenospondylus ninevehensis* exhibits a number of characters that make it an ideal antecedent to *C. casei*—1) more primitive dentition, 2) relatively shorter neural spines, 3) more typical sphenacodontine shape of its axial neural spine, and 4) smaller overall size. At first sight it might also be suggested that *Ctenospondylus* arose from *Sphenacodon* by merely tending toward a more exaggerated growth of its neural spines, the only prominent feature that separates these two genera; in relative spine length *C. ninevehensis* is

intermediate between *S. ferocior*, the most advanced species of *Sphenacodon* in which spine length is known, and *C. casei*. There are, however, a couple of facts that argue against such a relationship. *S. ferox* and *S. ferocior* follow one another in time and are undoubtedly directly related as a species lineage that extended from a horizon considered equivalent to the Woldcampian age lower parts of the Wichita Group to one considered equivalent to the early Leonardian age basal levels of the Clear Fork Group of Texas (Langston, 1953; Romer, 1960; Vaughn, 1964). Similarly, though *C. ninevehensis* existed at about the same time or very probably somewhat later than *C. casei*, it is reasonable to assume that *C. ninevehensis*, or something very close to it, must have preceeded *C. casei* phyletically during at least early Wolfcampian time. It would, therefore, appear that *Ctenospondylus* and *Sphenacodon* were independent lineages throughout the Early Permian. Further, *C. ninevehensis* exhibits a much greater primitiveness in its dentition than *S. ferox* or *S. ferocior* and, therefore, could not have been derived from either species. It should also be mentioned here that Vaughn (1964) has shown that in features of the atlantal centrum and the braincase *Sphenacodon* and *Dimetrodon* are closer to one another than either is to *Ctenospondylus*. Needless to say, the unusual structure of the neural spines of *Dimetrodon* eliminates even the remotest possibility of it having had a direct relationship with *Ctenospondylus*. The only other Lower Permian sphenacodontine whose possible relationships to *Ctenospondylus* need be discussed here is *Neosaurus cynodus*, a small European Autunian species known only by a maxilla from the Jura region of France (Romer and Price, 1940). Its possession of the unusually high number of four precanines that are separated from a single canine by a distinct, but low, maxillary step obviously places it as a primitive member of the sphenacodontines; its 10 postcanines, however, are more characteristic of the advanced sphenacodontines and set it widely apart from *Ctenospondylus*. The few poorly known Pennsylvanian sphenacodontines also appear to be more advanced than *C. ninevehensis*. From the late Stephanian of Kounova, Czechoslovakia, have come a number of bones that have been referred to a large sphenacodontine, *Macromerion schwarzenbergii* (Romer, 1945). The holotype is a partial maxilla and, although the marginal dentition is not complete, its tooth count was certainly significantly less than that of *C. ninevehensis*. Further, through comparison with a cast of the holotype of *M. schwarzenbergii*, it is also apparent that the maxilla of *C. ninevehensis* is considerably smaller and possesses a far less prominent canine swelling, which suggests a lesser development of the canines. Vaughn (1969) has described from the Late Pennsylvanian (probably Missourian) Sangre de Cristo For-

mation of Colorado an anterior portion of a maxilla retaining two anterior teeth that probably pertains to a very small sphenacodontine. Its most important diagnostic feature, as Vaughn (1969:24) points out, "is a 'step' in the maxilla such that the ventral edge of this bone anterior to the first tooth lies at a conspicuously higher level than does the rest of the ventral edge. The first tooth arises partly from the region of the step—this resembles the general condition in *Dimetrodon*." Though this specimen is much smaller than *C. ninevehensis*, it would appear that its maxillary step is more pronounced. Of the two teeth preserved in the Sangre de Cristo maxilla, undoubtedly the anterior one (6 mm long) is a precanine and the posterior one (11 mm long) a canine. Therefore, judging from Vaughn's description, it is very likely that the maxilla possessed only one, or at most two, precanines in contrast to the three seen in *C. ninevehensis*.

On what little information is available, it seems safest to assume for the present that *Ctenospondylus* became established as a distinct lineage by at least the Late Pennsylvanian and most likely arose from the haptodontine sphenacodonts. It is generally accepted that the Upper Pennsylvanian-Lower Permian haptodontines of Europe and North America, represented by the genera *Haptodus* (Romer and Price, 1940; Currie, 1977) and *Cutleria* (Lewis and Vaughn, 1965), are morphologically ideal ancestors to the sphenacodontines. As reasonably assumed by Currie (1977), the existence of a few poorly known or suspected sphenacodontines of Late Pennsylvanian age indicates that the ancestry of the haptodontines extends back to the Early or Middle Pennsylvanian. All of the haptodontine species are very close in structure and none exhibits any features to suggest a closer affinity to *Ctenospondylus* than to any other Lower Permian sphenacodontine.

It is not known whether the Dunkard *Ctenospondylus* represents a primitive holdover, as the above discussion might suggest, or whether it and the Utah and Texas representatives of this genus are members of separate lineages derived from a short-spined ancestor. In either case, the anachronistic appearance of *C. ninevehensis* lends support to the idea that some elements of the Dunkard fauna developed in isolation. Other faunal elements of the Dunkard can be cited in support of this viewpoint. The remarkable similarity between the amphibians *Diploceraspis* from the Upper Pennsylvanian and the Lower Permian Appalachian deposits and *Diplocaulus* from the Lower Permian of the southwestern United States, both noted for their bizarre "long-horned" skulls, has long been recognized (Beerbower, 1963) as a striking example of parallel evolution brought about by long-term separation. As will be reported in a future paper, a fairly good series of *Edaphosaurus* specimens is now available from throughout most of the Dunkard Group and an upper level of the underlying Monongahela

Group (considered uppermost Pennsylvanian by most). This series reveals differences from the well-documented evolutionary trends seen in the series of three consecutively occurring species of this genus, probably constituting a species phylum (Romer and Price, 1940), from the Texas Lower Permian. Although the Tri-state edaphosaur remains span a stratigraphic sequence that undoubtedly represents a considerable length of time, they do not appear to exhibit the marked increase in overall size with the time seen in the Texas species and remain within the size range of the earliest occurring Texas species, *E. boanerges*. Further, whereas in the Texas species the vertebral sail almost ceases to grow in absolute size, with later and larger species having proportionally smaller sails, those of the Tri-state edaphosaurs may increase slightly in proportion to body size with time but never attain the absolute size of the sail of *E. boanerges*. Certain of the structural trends in the neural spines of the Texas edaphosaurs, however, do seem to have been paralleled in those of the Monongahela-Dunkard edaphosaurs: 1) increased spacing and reduction in number of the tubercles of the neural spines, 2) flattening of the spine tips of the cervical vertebrae, and 3) a tendency for exuberant development of the distal-most tubercles of the spines in the cervical region.

Paleogeographic reconstructions also suggest an isolation of the Dunkard basin by the Late Pennsylvanian or the beginning of the Permian. The Dunkard basin can be thought of as a dying phase of a much larger Pennsylvanian Appalachian basin, which is typically viewed as having been a very shallow, swampy, northeastward extension of the Midcontinental seaway. It was along the eastern border of the Midcontinental seaway, which extended from Mexico to North Dakota during times of maximum advance, that the classic Lower Permian vertebrate-bearing beds of Texas and Oklahoma were deposited. It is, therefore, not unlikely that at times of maximum advance of the Appalachian arm of this seaway during the Early and Middle Pennsylvanian that an unbroken habitat zone, or zones, could have extended between the Tri-state and Midcontinental regions, providing a corridor for faunal movements. Paleogeographic reconstructions (McKee and Oriel et al., 1967) suggest, however, that with the close of the Pennsylvanian, expansion of areas of low relief may have formed a barrier, or at least a selective barrier, to faunal movements between these two regions. Unfortunately, this theory is not directly testable, because rocks of Late Pennsylvanian and Early Permian age have been removed by erosion from large parts of the central United States. The arm of the Midcontinental sea that had extended into the Appalachian geosyncline regressed southwestward by this time and any future transgressions would have probably been blocked by the further growth of existing positive areas that then completely bordered the eastern margin of the Midcontinent negative belt.

All that remained of the Appalachian basin at the onset of the Permian was the Dunkard basin. Sufficient stratigraphic and sedimentological information now exists (Arkle, 1959; Berryhill, 1967; Cross, 1975) to give a good overall picture of the physical environment of the Dunkard basin during this time. In general the Dunkard basin was a gently shelving, southwestwardly oriented, restricted basin of deposition that was bounded on the east and southeast by the active old Appalachia highlands, source of the Dunkard sediments, located on the then contiguous portions of southwestern Europe and northwestern Africa. On the west the basin was bordered by the stable continental interior, specifically the Cincinnati Arch, and separated from the Midcontinental basin complex by at least a thousand miles. With this paleogeographic setting in mind, it is easy to understand the possible occurrence of relictual or endemic forms in the Dunkard fauna.

ECOLOGY

The Nineveh Limestone undoubtedly represents a freshwater pond or lake environment. *Ctenospondylus* was a highly terrestrial and mobile genus and its preservation in this deposit was probably the result of its predation on the aquatic inhabitants of the "Nineveh" pond or lake. From the same site in which the Dunkard *Ctenospondylus* specimens were collected have also come a very large amount of remains, some partially articulated, of the amphibian *Trimerorhachis*, numerous isolated elements of the lungfish *Sagenodus*, and at least one bone, an ilium, that suggests the presence of an embolomere amphibian. Further, though the type skeleton of *C. ninevehensis* was disarticulated, its bones were preserved very close to one another and show no wear to suggest distant transport.

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